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Opportunity for female choice in the wild is frequently curtailed by low male trait variation in *Hyla versicolor*

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Abstract

To understand the efficacy of female choice in driving the evolution of male displays, we need to not only characterize preferences but examine the opportunity for the *expression* of such preferences. Mate assessment by females should be constrained if the relative attractiveness of multiple displays is perceived as equal because trait differences between them are indistinguishable. This is expected to result in apparently arbitrary mate choice, and knowledge about the frequency of such mating patterns is crucial in predicting the *strength* of sexual selection. Here, we examine discrimination abilities of female *Hyla versicolor* in the context of actual male-male chorus variation. We found that roughly half of mating encounters in the wild do not provide the call variation required for the expression of female preferences (non-arbitrary choice). Interestingly, the trait for which female *H. versicolor* shows the strongest preference during playback trials (call duration) is not the trait whose difference will most often be detectable to females in the wild (call rate). Furthermore, we document individual variation in discrimination ability, with some females being able to discriminate multiple traits, while others only focus on one trait. This suggests that the relatively high estimate of arbitrary mating is not only due to females struggling to discriminate natural local variation *overall* but due to an abundance of individuals with limited discrimination abilities that require encounters with males that differ in the specific trait they will discriminate. Lastly, small trait differences between males do not arise from nearest neighbors plastically altering their calls to be more similar. These findings provide insights on the frequently observed mismatch between laboratory phonotaxis and actual mating success in the wild.

Significance statement

How and why animals choose a mate are complicated questions. For many species (like the gray treefrog), we have good descriptions of the male advertisement and the female preferences. However, much less is known about the actual *expression* of such preferences in the wild, which rests on the opportunity for females to encounter perceptible variation among males. We determined the minimum acoustic differences necessary for females to detect a "more attractive" call and compared those abilities to male-male variation in the chorus. We predict that a female will encounter sufficiently disparate calls only half of the time, with all other choice events appearing to be arbitrary decisions (both calls sound equally attractive). This abundance of arbitrary mating is driven not only by low variation among males but also by wide disparity in discrimination abilities of females. These findings may explain why we often observe unexpectedly unpredictable mating patterns in other taxa.

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¹ Department of Biological Sciences, Behavioral and Molecular Ecology Group, University of Wisconsin-Milwaukee, Lapham Hall, 3209 N. Maryland Ave., PO Box 413, Milwaukee, WI 53201-0413, USA Keywords Female choice \cdot Mate preference \cdot Random mating \cdot Sexual selection \cdot Acoustic communication

Introduction

Mate choice is a major mechanism driving morphological and behavioral trait evolution (West-Eberhard 1983; Andersson 1994). The role of mate choice on sexual selection is usually examined by testing female responses to male traits across a spectrum of natural variation (i.e., preference functions) (Ritchie 1996; Jennions and Petrie 1997; Kilmer et al. 2017). When paired with corresponding male trait distributions, the shape of female preference functions can indicate the direction and strength of sexual selection (Gerhardt 2005; Gerhardt and Brooks 2009; Höbel and Gerhardt 2003).

The *existing* female preferences, however, may not predict realized choice outcomes, and factors affecting this expression of preferences in nature should limit the impact of female choice on sexual selection and trait evolution. There are a number of factors that can impair the expression of mate preferences in natural conditions. First, background noise generated by abiotic (wind, water) or biotic (conspecific or heterospecific signalers) sources can compromise female discrimination (birds: Catchpole and Slater 1995; anurans: Reichert and Ronacher 2015; Bee and Schwartz 2009; Bee et al. 2012; insects: Schmidt et al. 2011; Sueur 2002). Second, dense aggregations and the resulting low degree of spatial separation between males can reduce female capacity to identify attractive mates; as the perch distance or angular separation of two males decreases, female treefrogs are less able to distinguish between sound sources and localizing the more attractive call (Bee 2007; Richardson and Lengagne 2010). Third, the magnitude of variation among available males likely affects the ability of females to discriminate between them (Höbel 2015). We can expect a threshold below which the female no longer distinguishes between displays, either because they are too similar to merit a differential behavioral response or because they are too similar to be discriminated by her sensory or cognitive system (just meaningful/just noticeable difference; Nelson and Marler 1990). Moreover, the apparently widespread occurrence of categorical signal perception (anurans: Baugh et al. 2008; birds: Nelson and Marler 1989; insects: Wyttenbach et al. 1996) may further constrain the ability of females to differentiate between similar signals, particularly if alternatives fall on the same side of a perception boundary.

While the discrimination abilities (average discrimination thresholds for a given acoustic parameter) of crickets (von Helversen and Rheinlaender 1988) and anurans (Gerhardt et al. 1996; Gerhardt 1999; Murphy and Gerhardt 2000; Bee and Schwartz 2009; Kuczynski et al. 2010; Vélez et al. 2013) have been assessed through playback trials in controlled lab conditions, these findings are seldom compared to the actual signal variation available to females in the wild (but see Höbel 2015). While the population-wide range of natural variation in vocal displays is well described in many species of anurans (Hyla chrysoscelis, Schrode et al. 2012; Physalaemus pustulosus, Ryan and Rand 2003; Hya versicolor, Gerhardt et al. 1996), we emphasize the importance of characterizing variation at the spatial scales most relevant to mating decisions. If variation between advertising males perched in close proximity (and thus the likeliest candidates for discrimination) falls below this threshold,

we expect mate choice to be arbitrary. In this scenario, the resulting pattern of male mating success would resemble arbitrary mate choice, leading to very different implications for the strength of sexual selection on male displays. Thus, female preferences and discrimination thresholds should be placed in the context of neighbor-male variation and other aspects of chorus dynamics that could limit a female's ability to select the most attractive mate.

An aspect of chorus dynamics that may compound the problem of low magnitude of among neighbor variation is social plasticity in calling behavior. Males frequently adjust call parameters in accordance with chorus size, or even to "mimic" the qualities of nearby males (Gerhardt et al. 2000a, b; Schwartz et al. 2002; Reichert and Gerhardt 2012). Theoretically, if an unattractive male manages to adjust his call sufficiently to reduce the acoustic disparity to his more attractive neighbor, he may increase his chance of being chosen by an approaching female from 0% (for being unattractive) to 50% (having removed the ability of the females to choose between alternatives, her choice is expected to be arbitrary). This is likely more a problem for species in which mate choice is based on temporal rather than spectral call traits, since temporal traits show more social plasticity (Schwartz et al. 2002; Kime et al. 2004; Höbel 2015; but see Cunnington and Fahrig 2010). The number and diversity of taxa showing preferences for temporal traits (e.g., frogs: Rand and Ryan 1981; Schwartz and Wells 1984, 1985; Wells and Schwartz 1984; Kime et al. 2004; insects: Alexander 1975; Greenfield and Shaw 1983; fishes: Farr 1980; birds: Bradbury and Gibson 1983) suggest that social plasticity-induced weakening of between-male trait differences may be common, with the abovementioned consequences for mate choice and sexual selection.

Anuran amphibians are an excellent model for the study of sexual selection and mating signals. Mating decisions are based largely on acoustic signals (Ryan 2001; Gerhardt and Huber 2002) that can be easily replicated with artificial stimuli. Female treefrogs likely exhibit a "best of n" mate sampling strategy; they simultaneously assess a small number of nearby calls, meaning that limitations in discrimination and local variation are especially important in this taxon (as compared to "threshold" or "sequential search" strategies) (Murphy and Gerhardt 2002). And choice of preferred stimuli can be assessed in a straightforward way by taking advantage of the female phonotaxis behavior, which can be exploited during lab playback trials. In the wild, males gather in large choruses to call and attract females and socially-mediated plasticity in calling behavior has been described for many taxa, including H. versicolor (Schwartz et al. 2002; Kime et al. 2004; Reichert and Gerhardt 2012). While descriptions of male call variation and female call preferences are available for many species (Ryan 2001; Gerhardt and

Huber 2002), average call trait differences of neighboring males are rarely determined and consequently, it is not well understood how local male trait variation affects the opportunity for female choice in anurans or other taxa.

Here, we explore the opportunity for preference-based mate choice in eastern gray treefrogs (Hyla versicolor), by comparing the discrimination ability of females with the difference between potential mates they would encounter at the pond. Hyla versicolor is a common North American treefrog species and has been the focus of intense research on neurophysiological (Diekamp and Gerhardt 1995), behavioral (Runkle et al. 1994; Schwartz et al. 2001), and evolutionary (Sullivan and Hinshaw 1992; Gerhardt et al. 2000b; Gerhardt 2005; Reichert and Höbel 2015) aspects of mate choice and sexual selection. Female H. versicolor prefer longer calls, and calls delivered at shorter intervals (short call period) (Gerhardt et al. 2000b; Schwartz et al. 2001; Gerhardt 2005; Reichert and Höbel 2015). Females also show preferences for pulse rate, preferring higher rates provided that they are within the species-specific range (Gerhardt and Doherty 1988; GH, unpubl. data). The calling behavior of chorusing males is highly socially plastic (Wells and Taigen 1986; Schwartz et al. 2002; Reichert and Gerhardt 2012), but individual call properties vary in the magnitude to which males can adjust them: call duration and call period are plastic, while pulse rate is relatively fixed (likely because it is more involved in species recognition) (Gerhardt 1991; Schul and Bush 2002).

In Hyla cinera, a species in which mate choice is largely based on non-plastic, spectral call traits (Gerhardt 1987; McClelland et al. 1996; Höbel and Gerhardt 2003), a comparison of male call variation and female discrimination thresholds suggested that low variability among available mates should allow preference-based female choice in only 31% of mate choice encounters (Höbel 2015). We therefore hypothesized that the level of male display variation would have similar or worse effects on the opportunity for female choice in Hyla versicolor, and tested three predictions of this hypothesis. The first prediction is that females cannot or will not discriminate between two increasingly similar displays, i.e., that females have a discrimination threshold. The second prediction is that trait differences between displays of neighboring males are frequently below this female discrimination threshold. The third prediction deals with the effect of social plasticity on trait variation: because temporal call traits are more socially plastic, male call adjustments should exacerbate trait similarity; accordingly, species focusing on temporal call traits should show lower rates of preference-based female choice than species focusing on less socially plastic (i.e., spectral) traits. For H. versicolor, where temporal traits dominate, we thus predict lower than 31% opportunity for preference-based mate choice.

Methods

We conducted the analysis in five steps. (1) Determine female discrimination abilities. We evaluated female discrimination ability for three call traits by conducting two-choice playback trials in which females were presented with a series of attractive and unattractive alternatives that differed in their relative magnitude of difference. This generated population-level discrimination curves from which we obtained an estimate of the minimum trait difference at which females still showed preference-based choice (i.e., the trait difference at which a majority of females chose the attractive alternative). For a second sample of females, we additionally assessed individual variation in discrimination consistency. (2) Determine trait variation between males (for clarity, we use the term dvad in reference to nearest-neighbor pairs of competing signalers, so as not to be conflated with amplexed male-female pairs of frogs). (3) Combine information on male trait variation and female discrimination ability to estimate the proportion of male dyads that vary enough to be differentiated by females. (4) Use data on individual variation in discrimination ability to estimate how likely individual females are to encounter opportunities in which they can express preference-based choice. (5) Finally, compute trait differences between randomly generated male dyads and comparing those to the observed nearest-neighbor dyads to explore how much dyad trait differences are affected by plasticity in calling behavior (which should diminish differences between actual dyads, but not randomly selected ones).

Focal species and collection site

eastern gray treefrogs (*H. versicolor*) are frequently encountered in a range extending from Southeast Texas to the Upper Midwest and Northeastern region of the USA (Elliott et al. 2009).

Males have pulsed advertisement calls consisting of a series of short pulses that, at our test temperature of 20 °C, have a duration of approximately 25 ms and that are repeated after a pause of 25 ms (thus, at a given temperature, the duration of the call can be expressed in number of pulses or in ms). Average values (\pm SE) in our study population are call duration = 17 ± 0.5 pulses/call, call period = 5.936 ± 3027 ms, first frequency peak = 1071 ± 99 Hz, second (dominant) frequency peak = 2142 ± 192 Hz (data from N = 54 males recorded in 2011).

We collected data in May and June of 2017 at a pond adjacent to the University of Wisconsin–Milwaukee Field Station in Saukville, WI. Males were recorded at the pond, and females were collected in amplexed pairs and transported to the lab at the University of Wisconsin–Milwaukee. Because phonotaxis trials require exact knowledge of the presented call alternatives, it was not possible to record data blind. Pairs were kept in individual plastic containers (with 5 mm of water) in coolers on melting ice $(4-6 \text{ }^{\circ}\text{C})$ to prevent oviposition.

Determining female discrimination thresholds

Playback setup and stimulus generation

We conducted female choice trials in a sound-attenuated playback chamber at UWM (interior dimensions $3 \times 3 \times 2.4$ m). The testing arena was a circular enclosure measuring 2 m in diameter. The floor surface was assembled from foam play mats, and the 45-cm-high arena walls were made of wire fencing covered in black cloth. Two speakers (JBL CONTROL 1Xtreme) were placed behind the arena walls at two locations, each 1 m from the center. These speakers formed a 60° angle with the center of the arena, so as to imitate likely configurations of females approaching males from the pond edge (most males perch on the water surface deeper into the pond). The amplitude of each speaker was adjusted to 85 dB SPL using a Lutron SL-4001 sound level meter (Peak, 200 ms integration window). Signals were broadcast from a laptop connected to two Behringer A500 Reference Amplifiers (each controlling a single speaker). Females were released from the center of the arena using a wire cage (8 cm in diameter and 4 cm deep) attached to a pulley that could be activated from outside the testing chamber. We allowed individuals to move freely around the arena after the stimuli had played four times each. We recorded a response when a female entered a "choice zone"; a 20×9 cm rectangle directly in front of each speaker.

Stimuli were created using the R packages tuneR (Ligges et al. 2016) and Seewave (Sueur et al. 2008). Each stimulus varied for one of the three temporal call traits (with the other two held at population averages of 17 pulses, 20.5 pulses per second, and a call period of 5.936 s). Dominant and secondary frequency peaks were held at 2200 and 1100 Hz respectively, and amplitude of the second peak (1100 Hz) was attenuated by 10 dB (as is typical for the calls of this species). Pulse duration was held at 25 ms, rise and fall times were each 12 ms (i.e., when varying pulse rate, we only varied the silent interval between the pulses but kept the pulse duration constant).

Population-level discrimination thresholds by trait

We assessed the average limits of call differences below which the attractive call is no longer preferentially chosen (i.e., the discrimination threshold) using two-choice playback trials. Synthetic signals, varying for one of three call traits, were paired at five difference increments (5%, 10%, 15%, 20%, and 25%), centered around the population mean (Table 1). By manipulating one trait while holding the others constant at population averages, we created three univariate sets of two-choice trials. Each female thus participated in 15 trials (5 trials varying in degree of difference, for 3 call traits). Using preference functions from our study population (call duration and call period: Reichert and Höbel 2015; pulse rate: R.C. Kolodziej and GH, unpubl. data), an "attractive" option (having more pulses, faster pulse rate, or shorter call period) was designated for all signal pairings. A female's response in each trial was recorded in a binary fashion: "attractive (1)" or "unattractive (0)".

For each call trait, we assembled discrimination curves, which show the proportion of females choosing the attractive alternative as a function of the magnitude of the call difference (on a 5–25% difference scale). Because at a sample size of N=20 a binomial test will result significant if more than 14 females approach a given alterative (>70% of the sample), we selected this as the cutoff that we considered the discrimination threshold for the given trait.

The discrimination curve for call duration, with alternatives varying around our population average (17 pulses), was very flat (see "Results"). Because the preference functions for call duration (number of pulses) are open ended but does plateau once values slightly exceed the population mean (Gerhardt et al. 2000b; Reichert and Höbel 2015), we subsequently tested another 16 females at 5%, 15%, and 25% difference increments when stimuli were both in the "unattractive" range of the preference function, that is, with the short alternative set at a mere 6 pulses (Table 1, italicized values). We expected that females would show finer discrimination when confronted with the lower extreme of the trait spectrum (also observed in H. chrysoscelis; Ward et al. 2013). These trials were meant as a control to test whether females are capable of discriminating a certain pulse number difference yet chose not to because both alternatives in the tests centering around average values were all perceived as sufficiently attractive. We note that Weber's law, which states that the ability to discriminate two stimuli depends on the proportional difference between them, also predicts that short-duration pairings are easier to discriminate than the average-duration ones. However, the shape of the preference function for call duration, with its pronounced drop towards very short calls (Reichert and Höbel 2015), indicates departure from Weber's law, which has also been highlighted in other studies examining call duration preferences in *H. versicolor* (Gerhardt et al. 2000b; Bee 2008).

Examining variation and consistency in individual-level discrimination

To examine potential among-female variation in discrimination ability, as well as an individual's consistency in choosing the attractive option (given that they can detect it), we conducted a second experiment. Here, we tested 16 additional females 5 times each at a fixed difference level of 20% (the previously established thresholds for each of three traits; see "Results"). Each female thus participated in 15 trials (5

 Table 1
 Call parameters (top row) and value pairings used in female choice playback trials.

 Alternate call duration (short call) pairings are italicized

	Call duration (no. of pulses)	Pulse rate (pulses/s)	Call period (ms)
Mean	17	21	6088
5% difference	16–17 (6–7)	20-21	5784-6088
10% difference	16–18	19–21	5784-6392
15% difference	15–18 (6–9)	19–22	5480-6392
20% difference	15–19	18–22	5480-6696
25% difference	14–19 (6–11)	18–23	5176-6696

repeated trials for 3 call traits). If a female chose the attractive option at least 4 out of 5 times, she met the criterion for being "discriminatory," while those that showed lower sums were interpreted as being "non-discriminatory" (we use the term "consistency" in a strictly categorical sense). Having tested discrimination ability for three traits in each female, we were also able to examine whether discriminatory performance is related among call parameters (i.e., if females that consistently discriminate call duration are likely to discriminate pulse rate and/or call period as well). We also tested for differences among females' scores in a two-way ANOVA using restricted maximum likelihood (REML). This analysis included female consistency scores (on a scale of 1-5, depending how often she chose the attractive stimulus in a given trait category (pulse number, call period, pulse rate)) as the test variable, and trait, individual female identity (random effect), and their interaction, as factors in the analysis. This analysis provides confidence intervals, and CI not overlapping zero indicate significant effects.

Between-male call variation

Analysis of call recordings

We recorded a total of 84 males using a TASCAM DR-100MKII Linear PCM Recorder (TEAC Corporation, Tokyo Japan) and a Sennheiser K6+ME66 directional microphone. Each individual's "nearest neighbor" was defined as the closest frog signaling at the same time as the focal male, and frogs were only recorded when their neighbor was calling simultaneously in order to capture potential effects of plasticity in calling behavior. We measured nearest-neighbor perch distances using a Foneso F100 Laser Distance Meter. We did not use a pre-determined cutoff distance for deciding whether two males were nearest neighbors; some species establish calling perches based on call amplitude of rival males located well over 5 m (Wilczynski and Brenowitz 1988), suggesting that they attend to other males at quite large distances. Rather, we aimed to capture the variation of inter-male distances at the pond and then test for a potential distance threshold beyond which acoustic "mimicry" is not detected. This resulted in 55 "dyads" of males sampled opportunistically during ten nights of chorus activity spanning that year's breeding season.

Although body size and body temperature are covariates with some call traits, these variables were not recorded because we were interested only in capturing the real-world variation perceived by approaching females. We did, however, take one temperature measure each night before commencing to record male calls (22:00 h, air temperature, shoreline). In addition, for every night in which frogs were recorded, we scored nightly chorus size (according to the three-category North American Amphibian Monitoring Program scale). This allowed us to later test whether nearest-neighbor distance or chorus size affected call trait difference between male dyads.

Call recordings were analyzed using Audacity software. We examined call duration (in number of pulses), pulse rate (in number of pulses per second), and call period (in seconds, defined as time elapsed between the start of one call and the start of the subsequent call), calculating averages across approximately 9 calls per individual (call period, 8.87 calls \pm 1.32; call duration and pulse rate, 9.49 calls \pm 0.92, range of 5 to 10 calls).

Quantifying call variation

We quantified call trait variation following Höbel (2015). Here, call trait differences for each nearest-neighbor dyad are divided by the population means (Mean_{POP}), resulting in dimensionless scores that facilitate comparison across traits:

 $Diff_{NN} = (ABS(Mean_{Male1} - Mean_{Male2})/Mean_{POP}) \times 100$ where $Mean_{POP}$ is the population average for each call trait (duration, pulse rate, and period) and ABS is the absolute value.

Perch distances and chorus density

To test for potential effects of nearest-neighbor proximity on within-dyad call trait variation (Diff_{NN}), we performed a linear regression. Additionally, we examined chorus density effects by performing ANOVA on Diff_{NN} and chorus size (NAAMP category 1 through 3).

Estimating opportunity for female choice

Using data on population-based discrimination thresholds (20% difference, see "Results"), we determined the quantity

of male-male dyads that fell below (too similar) or above (sufficiently varied) this boundary. These tallies provide estimates of the frequency of predictable, preference-driven mate choice in the population.

Using data on the variation and consistency of discriminatory behavior of individual females, we tallied each female's "likelihood of encountering a sufficiently varied dyad," based on her response to each of the three examined call traits. For example, a female that is not discriminatory for traits except call period would receive a likelihood based on the number of male dyads that fall above the call period threshold alone. Likewise, a female exhibiting discrimination across all three traits would be expected to choose the more attractive male in all dyads that vary sufficiently for any one of the three measured traits. This does not, however, lead to the expectation that such females will be three times as likely to exhibit preference-based choice because there will often be redundancy among dyads that fall above their thresholds for each trait (some male dyads will differ for multiple traits simultaneously). Such females were likewise scored as being "expected to discriminate" any dyads that exhibited > 20% in any one trait.

Population-wide test for plasticity

We explored the potential impact of social plasticity on local call variation by computing male trait differences between randomly generated male dyads and comparing those to the observed nearest-neighbor dyads. We generated a data set of call trait differences of random-neighbor dyads (Diff_{RN}) by randomly assigning a competitor to a focal male. Here, each recorded male served as focal males once and the competitor was chosen from the pool of males that were recorded during a comparable chorus night (blocked by chorus size and nightly air temperature). This generated "dyads" that lacked the potential for being influenced by social plasticity in calling behavior, i.e., these calls cannot be adjusted to the other signaler.

We predicted that traits affected by social plasticity (adjustments to mimic competing signals) would show reduced male-male differences when dyads were based on actual proximity rather than to a randomly assigned neighbor. We calculated ANOVA to test for a difference in mean male-male disparity between nearest-neighbor and random-neighbor cohorts. Percent differences were arcsin square-root transformed before analysis.

Data availability

All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Results

Female discrimination abilities

Population-level discrimination thresholds

For a significant proportion of females to approach the more attractive alternative, the call period and pulse rate stimuli had to differ by more than 20%. Call duration stimuli centered around the population mean were not significantly discriminated even at the highest difference level we tested (25%, i.e., 14 vs 19 pulses/call). When we repeated the call duration trials using alternatives shifted to the short (unattractive) end of the trait spectrum, near-total discrimination for the longer call occurred at the 15% difference magnitude (Fig. 1).

Discrimination and consistency at individual female level

The percent of females that passed the criteria for "demonstrating consistent discrimination" (i.e., chose the



Magnitude of trait difference [%]

Fig. 1 Summary of results from population-level testing of female discrimination. The *x*-axis shows the spectrum of call disparities presented in two-choice traits, and the *y*-axis shows the proportion of females that correctly chose the more attractive stimulus. Curve lines represent spline-plots of the proportion of females that chose the attractive stimulus (**a**: longer duration; **b**: shorter periods; and **c**: higher rates) at each

respective magnitude of trait difference; thinner lines represent ± 1 SE. A second gray curve (call duration only) represents results of testing for discrimination against short calls. Horizontal lines indicate the thresholds at which discrimination is 50% (random choice) and 70% (above which we see statistically significant preference). Vertical lines indicate the threshold of discrimination by trait

more attractive alternative at least 4 out of 5 times) was 69% for call duration, 62% for call period, and 75% for pulse rate (Fig. 2). These proportions around 70% indicate that females are quite consistent in their discrimination ability. Remember that we had tested these individuals at a difference magnitude (20% difference) at which not all but only a significant proportion (70%, see above) of females in the population had chosen the more attractive alternative.

Using this data on individual performance, we found that all females were able to discriminate alternatives in at least one of the three tested call traits (Fig. 3). Roughly 30% of individuals even showed across-the-board acuity for all three call traits. We do not report a conventional measure of repeatability here, because the design of this experiment does not allow for consistent among-female variation (they can only exhibit repeatable preference for a common attractive stimulus). In a two-way ANOVA (REML method), the variance from individual identity generated confidence intervals that overlapped zero (expected from our experimental design, see above). However, the individual \times trait interaction term was significant (Var. comp. = 0.038, 95% CI = 0.025–0.069). This indicates that, while females did not appear to consistently differ in general performance, they did vary in which trait(s) they discriminated best.

Male call variation and within-dyad call differences

Across a total sample of 84 males, the average call was 18 pulses (range, 10.7-33.4 pulses), with a call period of 6.7 s (range, 1.9-17.1 s) and a pulse rate of 20.6 pulses/s (range, 14.6-28.1 p/s) (Fig. 1).

In the sample of 54 dyads of nearest-neighbor males (15 individuals participated in two dyads; one male participated in three), average difference for call duration was 16.1% (range, 0.4–61.9%); for call period, it was 32.5% (range, 1.9–173.6%); and for pulse rate, it was 6.5% (range, 0.1–25.3%). Average between-male perch distance was 3.7 m (range of 0.25–15.2 m), and nearest-neighbor distances were shorter in larger choruses ($F_{2.51} = 7.12$, p = 0.002). All recorded males

were used as a "focal male" in comparison with their respective closest neighbor.

Within-dyad call trait differences (Diff_{NN}) were neither affected by the perch distance between nearest neighbors (call duration $F_{1,52} = 0.01$, p = 0.94; call period $F_{1,52} = 0.12$, p = 0.73; pulse rate $F_{1,52} = 1.73$, p = 0.19), nor by chorus size (call duration $F_{1,52} = 0.22$, p = 0.81; call period $F_{1,52} = 0.22$, p = 0.80; pulse rate $F_{1,52} = 0.49$, p = 0.62).

Estimated effect of call plasticity on within-dyad differences

Average within-dyad difference was significantly higher in the randomly paired (Diff_{RN}) compared to the nearest neighbor (Diff_{NN}) data set for pulse rate ($F_{1,166} = 5.16$, p = 0.02). Call duration ($F_{1,166} = 0.33$, p = 0.57) or call period ($F_{1,166} = 0.57$, p = 0.45) differences, however, were not different between the two data sets.

Estimating opportunity for female choice

Using the *population-based* discrimination data set, we estimate that 33% of the recorded dyads were too similar to allow preference-based female choice. Sixty seven percent of the 55 dyads differed sufficiently for at least a single trait, 50% differed for two traits, and 7% differed for all three. The call trait that most often differed sufficiently to enable female discriminatory choice for the attractive male was call period, with 56% of male dyads being above threshold. Call duration was the second most different trait (35% of dyads differing sufficiently), while pulse rate was almost never sufficiently different (5% of dyads) (Fig. 4). Assuming that above-threshold differences in *any* one trait are sufficient for preferencebased female choice, we therefore estimate that approaching females would consistently choose the attractive male in 67% of the recorded male dyads.

A more refined estimate of the opportunity for female choice can be obtained by looking at the consistency of discrimination behavior of individual females and comparing this



Fig. 2 Results of individual-level discrimination trials using repeatedstimulus design. Histogram categories represent the sum of correct responses (out of 5 total) achieved by each female (n = 16). Females scoring

at least 4 out of 5 correct responses (gray shading) met the criteria for discrimination of a given trait



Fig. 3 Summary of individual female performance in discrimination trials across traits. Most females exhibit a discrimination ability for multiple traits



Fig. 4 Comparison of female discrimination thresholds to male-male trait differences for (**a**) call duration, (**b**) pulse rate, and (**c**) call period. Distributions of neighboring males by corresponding difference magnitudes are shown in histograms. Individual males (circles) are plotted along the trait spectrum by difference magnitude, with nearest neighbor pairings indicated by lines. Shaded regions of the graph represent the difference threshold at which females exhibited >70% discrimination. Additional shading on the call duration graph represents finer discrimination against shorter calls (see Fig. 1)

to the available male dvads. Using the *individual-based* discrimination data set, we estimate that the chance of an approaching female to encounter a male dyad that differed sufficiently to allow preference-based mate choice ranged from as low as 35% to as high as 70% (mean \pm SE 54% \pm 3.65%). This range is a function of how many traits each female is able to differentiate (remember that some females only discriminate one trait, while others discriminate all three). The lower estimate is based on the calculation that "one-trait" females had at least a 35% chance to encounter a male dyad that differed sufficiently in the single trait they could differentiate, while the upper estimate reflects the chance of "three-trait" females of encountering dyads that differed in any one of the traits they could differentiate (the average estimate reflects the chances of one, two, and three trait females, respectively). Our "refined" estimate is therefore that approaching females will consistently choose the attractive male in 54% of the recorded male dyads.

We had hypothesized that social plasticity in calling behavior decreases within-dyad variation between nearest-neighbor males, thus impairing female discrimination. To estimate the effect that social plasticity in calling behavior has on the opportunity for mate choice, we recalculated the individual female "discrimination likelihoods" by comparing them to the hypothetical population of dyads of randomly paired males. The average likelihood of encountering dissimilar dyads increased slightly to 59% (range, 32–78%), suggesting that the contribution of social plasticity to trait similarity in this population is noticeable but small.

Discussion

A key assumption of sexual selection by female choice is that the male with the more attractive display gains higher mating success. This, however, relies on females being able to reliably identify and copulate with the more attractive male. We examined the minimum call differences that female *H. versicolor* require to choose the more attractive call, and compared it to call difference between neighboring males. This allowed us to estimate how often more attractive males at our study pond should be chosen by an approaching female, compared to how often mating success is expected to be equalized by females not differentiating between similar males. We estimate that the magnitude of between-male differences available at our site will result in nearly equal occurrences of arbitrary and preference-based mate choice.

Implications for sexual selection

Finding that many females will not be able to choose the more attractive male at the observed between-male call differences at our pond has several implications for sexual selection. First, the low call variation suggests that strong selection in the past has brought our population close to equilibrium, with most males being sufficiently attractive to satisfy approaching females. This is especially the case for the trait call duration; females discriminate strongly against calls with fewer than 12 pulses, but such unattractive short calls are rarely observed in our populations. By contrast, the frequent occurrence of arbitrary mate choice under current conditions should lower the overall *strength* of selection (but not its *direction*), thus maintaining some degree of trait variation in the current population.

Second, our data underscores the notion that, to fully understand how sexual selection by female choice is currently acting in nature, information from lab preference trials have to be interpreted in conjunction with information about the male display variation females are likely to encounter during mate choice. Playback trials consistently identify call duration as the call property for which female H. versicolor have the strongest preference (Welch et al. 1998; Gerhardt et al. 2000b; Reichert and Höbel 2015). This would suggest that call duration is the trait that females will use to choose among potential mates. However, because call duration differences between neighboring males are often below the female discrimination threshold, we suggest that mate choice in nature is likely more often driven by call period differences, which shows larger between-male variation. Consequently, mate choice in nature may be mostly driven by the trait that females can more easily differentiate (here, call period), not by the one for which they have the strongest preference (here, call duration).

Call duration and call period are frequently correlated, creating the well-known trade-off where an attractive long call has to be produced at an unattractive slow rate, and vice versa (Ward et al. 2013, but see Reichert and Gerhardt 2012). Both traits also show social plasticity, i.e., males often adjust their duration or rate to those of neighbors (Wells and Taigen 1986; Schwartz et al. 2002). Based on preference data alone, the stronger preference for call duration relative to call period suggests that a male could increase his attractiveness more by prolonging his call than by increasing how frequently he is calling. Given the conditions at our pond, however, where males are too similar in call duration to be discriminated, the opposite strategy might be more adaptive-call more often, even if that means decreasing call duration a bit (while remaining below discrimination threshold differences). Then again, the huge range of call periods we found at our pond also implies that, in many instances, the disparity between two neighboring males is too vast for plastic adjustments to effectively change relative attractiveness.

Finally, we think that discrimination ability is a factor that frequently plays a role in determining mate choice in nature. Though it is rarely the explicit subject of preference trials, it is often possible to infer discrimination ability from those studies. A few species seem to be able to discriminate call differences at lower thresholds than reported here (see Gerhardt et al. 2000b; Bee and Schwartz 2009; Vélez et al. 2013). Females from a Missouri population of gray treefrogs, for example, were able to detect a 2-pulse difference in call duration (roughly 10% difference magnitude) (Gerhardt and Watson 1995). While some of our more discriminant individuals may achieve such accuracy, we found no evidence that females overall show preference at this level of similarity. In general, however, the call trait discrimination abilities of anurans are comparable to those in our study (Gerhardt and Doherty 1988; Gerhardt 1991; Gerhardt 1999; Murphy and Gerhardt 2000; Höbel 2015). Should male call variation in these species be similarly low as reported for H. versicolor (this study) and H. cinerea (Höbel 2015), then incidents of arbitrary mate choice resulting from females not differentiating between similar males should be a common occurrence, and frequently curtail the strength of sexual selection in nature below what would be estimated from preference trials alone. This limitation is especially relevant when the expected sampling strategy is "best of n," as observed in H. gratiosa (Murphy and Gerhardt 2002).

Population-based versus individual-based variation in discrimination ability

Based on population-level averages of discrimination ability, we predicted that preference-based mate choice would be expected in 67% of encounters at our pond. While population patterns can give important insight to mate choice behavior and their effect on sexual selection, there is a growing body of literature documenting the existence of substantial among-female variation in a range of female preference traits (i.e., choosiness, peak preference, preference function shape; (Murphy and Gerhardt 2000; Kuczynski et al. 2017; Neelon and Höbel 2017; D.P. Neelon and GH, unpubl. data).

By employing repeated-measure design to the evaluation of discrimination thresholds, we demonstrate that there is also considerable among-female variation in discrimination ability. When considering this individual-level discrimination ability, we instead predict roughly equal occurrences of preferential (54%) and arbitrary (46%) mate choice. "Three-trait" females have a higher chance of selecting the more attractive male, assuming that they can do so as long as differences in any one of those traits surpass the threshold. "One-trait" females, on the other hand, are more likely to choose higgledy-piggledy, because they will only be able to select the more attractive male if the dyads they encounter differ in the specific focus trait. It is clear that certain individuals are simply more discriminating when confronted with variation in sexual displays and the individual-level exploration of these abilities leads to more robust predictions about the occurrence of nonarbitrary mating (see also Wagner 1988). Apparently

random mate choice would result not only from low local trait variation (as suggested by Höbel 2015) but also by the presence of a certain proportion of females that require that the males they encounter differ in a very specific trait in order to express choice.

While some individuals can discriminate multiple traits if they differ by 20%, others show highly restricted assessment and discriminate only a single trait at this difference magnitude. Consequently, just as calls can differ in a number of call traits, females are not expected to perceive the difference of the calls of two males in the same way. Rather, individuals may differ in their assignment of an "attractive" versus an "unattractive" signaler, based on the particular traits they focus on. These insights contribute to a growing body of anuran research on among-individual variation in mate choice (Baugh and Ryan 2009; Gall et al. 2019; Neelon et al. 2019). Here, we only tested if females can consistently tell the difference at a relatively large difference (20%). It would be interesting to see whether females that focus on only one or two traits are better at discriminating those traits at a finer scale (i.e., can "onetrait" females tell the more attractive male already when this trait differs by 5% difference, while "three-trait" female only do so only at 20% difference). This is a phenomenon that merits further study, as it should affect sexual selection.

Social plasticity of male calling behavior and its effect on female ability to discriminate between males

Temporal call traits generally show a higher degree of plasticity than spectral ones (McClelland et al. 1996), and this plasticity is frequently socially mediated (Wells and Taigen 1986; Kime et al. 2004; Reichert and Gerhardt 2012). The expectation that call differences should be reduced as males adjust their calls to those of their neighbors led us to predict that species that emphasize temporal call traits for mate choice (such as the H. versicolor) would encounter fewer male dyads differing by the required magnitude, and consequently show comparatively lower occurrences of preference-based mate choice. This was not the case, however. Höbel (2015) calculated that H. cinerea females (a species focusing on call frequency) should exhibit preference-based choice in only 31% of dyad encounters. Using the same (population-based) calculation of discrimination ability, we estimate that, in H. versicolor, preference-based choice would occur in 67% of encounters (note also that our individual-based estimate for H. versicolor is lower than that, but still above the estimate, for H. cinerea).

The above result, suggesting that species focusing on temporal call traits do not face greater assessment challenges arising from call similarity, has one caveat, however. Although male anurans, including those from other populations of *H. versicolor* (Gerhardt et al. 1996), have been reported to adjust their calls to those of nearest neighbors (Schwartz et al. 2002; Reichert and Gerhardt 2012) as well as to local chorus density (Schwartz et al. 2002; Love and Bee 2010), we found very little evidence for this in our study: within-dyad call trait differences were neither affected by the perch distance between nearest neighbors nor by chorus size. This apparent lack of a social component influencing call differences was further underscored by the results of our randomneighbor simulation: the actual survey of male dyads, where males could hear each other and presumably adjust to each other's displays, did not show smaller call duration or period differences than a hypothetical sample of randomly paired calls. While we did observe statistically smaller male-male disparities in pulse rate, it is possible that this result is spurious; having recorded perch temperatures of individual males allowing for later temperature correction of call parameters may have pointed to similar temperatures as the main driver behind similar pulse rates of neighboring males.

Conclusion

Observations of male mating success in the wild frequently do not line up with female preference data (Gerhardt et al. 1987; Arak 1988; Morris 1989; Sullivan and Hinshaw 1992; Møller and Alatalo 1999; Smith and Roberts 2003; Friedl and Klump 2005). Our study provides a potential explanation for this long-standing puzzle. If females only differentiate trait differences of a magnitude that is often not encountered in nature, a high proportion of apparently arbitrary mate choice is in fact the expected pattern we should find in many populations. The strength of sexual selection should be further eroded by female variation in discrimination ability, as it requires not only that the approaching female encounters males whose traits differ by a sufficient magnitude but also that they differ in the particular trait(s) the female compares.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. The Institutional Animal Care and Use Committee of UWM approved the use of these treefrogs (protocol # 16-17 #19).

References

- Alexander RD (1975) Natural selection and specialized chorusing behavior in acoustical insects. In: Pimentel D (ed) Insects, science, and society. Academic Press, New York, pp 35–77
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Arak A (1988) Female mate selection in the natterjack toad: active choice or passive attraction? Behav Ecol Sociobiol 22:317–327
- Baugh AT, Ryan MJ (2009) Female túngara frogs vary in commitment to mate choice. Behav Ecol 20:1153–1159
- Baugh AT, Akre KL, Ryan MJ (2008) Categorical perception of a natural, multivariate signal: mating call recognition in túngara frogs. Proc Natl Acad Sci U S A 105:8985–8988
- Bee MA (2007) Sound source segregation in grey treefrogs: spatial release from masking by the sound of a chorus. Anim Behav 74:549– 558
- Bee MA (2008) Parallel female preferences for call duration in a diploid ancestor of an allotetraploid treefrog. Anim Behav 76:845–853
- Bee MA, Schwartz JJ (2009) Behavioral measures of signal recognition thresholds in frogs in the presence and absence of chorus-shaped noise. J Acoust Soc Am 126:2788–2801
- Bee MA, Velez A, Forester JD (2012) Sound level discrimination by gray treefrogs in the presence and absence of chorus-shaped noise. J Acoust Soc Am 131:4188–4195
- Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 109– 138
- Catchpole CK, Slater PJB (1995) Bird song: biological themes and variations. Cambridge University Press, Cambridge
- Cunnington GM, Fahrig L (2010) Plasticity in the vocalizations of anurans in response to traffic noise. Acta Oecol 36:463–470
- Diekamp B, Gerhardt HC (1995) Selective phonotaxis to advertisement calls in the gray treefrog *Hyla versicolor*: behavioral experiments and neurophysiological correlates. J Comp Physiol A 177:173–190
- Elliott L, Gerhardt HC, Davidson C (2009) The frogs and toads of North America: a comprehensive guide to their identification, behavior, and calls. Houghton Mifflin Harcourt, Boston
- Farr JA (1980) Social behaviour patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae): an experiment on the effects of intermale competition, female choice and sexual selection. Behaviour 74:38–91
- Friedl TWP, Klump GM (2005) Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. Anim Behav 70:1141–1154
- Gall M, Bee M, Baugh AT (2019) The difference a day makes: breeding remodels hearing, hormones and behavior in female Cope's gray treefrogs (*Hyla chrysoscelis*). Horm Behav 108:62–72
- Gerhardt HC (1987) Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, *Hyla cinerea*. Anim Behav 35:1479–1489
- Gerhardt HC (1991) Female mate choice in treefrogs: static and dynamic acoustic criteria. Anim Behav 42:615–635
- Gerhardt HC (1999) A quantitative analysis of behavioral selectivity for pulse rise-time in the gray treefrog, *Hyla versicolor*. J Comp Physiol A 185:33–40
- Gerhardt HC (2005) Advertisement-call preferences in diploid-tetraploid treefrogs (*Hyla chrysoscelis* and *Hyla versicolor*): implications for mate choice and the evolution of communication systems. Evolution 59:395–408
- Gerhardt HC, Brooks R (2009) Experimental evidence of multivariate female choice in gray treefrogs (*Hyla versicolor*): evidence for directional and stabilizing selection. Evolution 63:2504–2512

- Gerhardt HC, Daniel RE, Perrill SA, Schramm S (1987) Mating behaviour and male mating success in the green treefrog. Anim Behav 35: 1490–1503
- Gerhardt HC, Doherty JA (1988) Acoustic communication in the gray treefrog, *Hyla versicolor*: evolutionary and neurobiological implications. J Comp Physiol A 162:261–278
- Gerhardt HC, Huber F (2002) Acoustic communication in insects and frogs: common problems and diverse solutions. University of Chicago Press, Chicago
- Gerhardt HC, Watson GF (1995) Within-male variability in call properties and female preference in the grey treefrog. Anim Behav 50: 1187–1191
- Gerhardt HC, Dyson ML, Tanner SD (1996) Dynamic properties of the advertisement calls of gray tree frogs: patterns of variability and female choice. Behav Ecol 7:7–18
- Gerhardt HC, Roberts JD, Bee MA, Schwartz JJ (2000a) Call matching in the quacking frog (*Crinia georgiana*). Behav Ecol Sociobiol 48: 243–251
- Gerhardt HC, Tanner SD, Corrigan CM, Walton HC (2000b) Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). Behav Ecol 11:663–669
- Greenfield MD, Shaw KC (1983) Adaptive significance of chorusing with special reference to the Orthoptera. In: Gwynne DT, Morris GK (eds) Orthopteran mating systems: sexual competition in a diverse group of insects. Westview Press, Boulder, CO, pp 1–27
- Höbel G (2015) Female discrimination thresholds frequently exceed local male display variation: implications for mate choice dynamics and sexual selection. J Evol Biol 29:572–582
- Höbel G, Gerhardt HC (2003) Reproductive character displacement in the communication system of green treefrogs (*Hyla cinerea*). Evolution 57:894–904
- Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–327
- Kilmer JT, Fowler-Finn KD, Gray DA, Höbel G, Rebar D, Reichert MS, Rodríguez RL (2017) Describing mate preference functions and other function-valued traits. J Evol Biol 9:1658–1673
- Kime NM, Burmeister SS, Ryan MJ (2004) Female preferences for socially variable call characters in the cricket frog, Acris crepitans. Anim Behav 68:1391–1399
- Kuczynski MC, Velez A, Schwartz JJ, Bee MA (2010) Sound transmission and the recognition of temporally degraded sexual advertisement signals in Cope's gray treefrog (*Hyla chrysoscelis*). J Exp Biol 213:2840–2850
- Kuczynski MC, Getty T, Gering E (2017) Larger females are choosier in the gray treefrog (*Hyla versicolor*). Behav Process 135:29–35
- Ligges U, Krey S, Mersmann O, Schnackenberg S (2016) tuneR: analysis of music. http://r-forge.r-project.org/projects/tuner/
- Love EK, Bee MA (2010) An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog (*Hyla chrysoscelis*). Anim Behav 80:509–515
- McClelland B, Wilczynski W, Ryan M (1996) Correlations between call characteristics and morphology in male cricket frogs (*Acris crepitans*). J Exp Biol 199:1907–1919
- Morris MR (1989) Female choice of large males in the treefrog Hyla chrysoscelis: importance of identifying the scale of choice. Behav Ecol Sociobiol 25:275–281
- Møller AP, Alatalo RV (1999) Good-gene effects in sexual selection. Proc R Soc Lond B 266:85–91
- Murphy CG, Gerhardt HC (2000) Mating preference functions of individual female barking treefrogs, *Hyla gratiosa*, for two properties of male advertisement calls. Evolution 54:660–669
- Murphy CG, Gerhardt HC (2002) Mate sampling by female barking treefrogs (*Hyla gratiosa*). Behav Ecol 13:472–480
- Neelon DP, Höbel G (2017) Social plasticity in choosiness in green tree frogs, *Hyla cinerea*. Behav Ecol 28:1540–1546

- Neelon DP, Rodriguez RL, Höbel G (2019) On the architecture of mate choice decisions: preference functions and choosiness are distinct traits. Proc R Soc B 286:20182830
- Nelson DA, Marler P (1989) Categorical perception of a natural stimulus continuum: birdsong. Science 244:976–978
- Nelson DA, Marler P (1990) The perception of bird song and an ecological concept of signal space. In Stebbins WC, Berkeley MA, editors. Comparative perception. New York: John Wiley. p. 443–78.
- Rand AS, Ryan MJ (1981) The adaptive significance of a complex vocal repertoire in a neo- tropical frog. Zeitschr Tierpsychol 57:209–214
- Reichert MS, Gerhardt HC (2012) Trade-offs and upper limits to signal performance during close-range vocal competition in gray tree frogs *Hyla versicolor*. Am Nat 180:425–437
- Reichert MS, Höbel G (2015) Modality interactions alter the shape of acoustic mate preference functions in gray treefrogs. Evolution 69: 2384–2398
- Reichert MS, Ronacher B (2015) Noise affects the shape of female preference functions for acoustic signals. Evolution 69:381–394
- Richardson C, Lengagne T (2010) Multiple signals and male spacing affect female preference at cocktail parties in treefrogs. Proc R Soc Lond B 277:1247–1252
- Ritchie MG (1996) The shape of female mating preferences. Proc Natl Acad Sci U S A 93:14628–14631
- Runkle LS, Wells KD, Robb CC, Lance SL (1994) Individual, nightly, and seasonal variation in calling behavior of the gray tree frog, *Hyla versicolor*: implications for energy expenditure. Behav Ecol 5:318– 325
- Ryan MJ (2001) Anuran communication. Smithsonian Institution Press, Washington DC
- Ryan MJ, Rand AS (2003) Sexual selection in female perceptual space: how female túngara frogs perceive and respond to complex population variation in acoustic mating signals. Evolution 57:2608–2618
- Schmidt AKD, Riede K, Römer H (2011) High background noise shapes selective auditory filters in a tropical cricket. J Exp Biol 214:1754– 1762
- Schrode KM, Ward JL, Velez A, Bee MA (2012) Female preferences for spectral call properties in the western genetic lineage of Cope's gray treefrog (*Hyla chrysoscelis*). Behav Ecol Sociobiol 66:1595–1606
- Schul J, Bush SL (2002) Non-parallel coevolution of sender and receiver in the acoustic communication system of treefrogs. Proc R Soc Lond B 269:1847–1852
- Schwartz JJ, Wells KD (1984) Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. Behav Ecol Sociobiol 14:211– 224
- Schwartz JJ, Wells KD (1985) Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala*. Copeia 1985:27–38
- Schwartz JJ, Buchanan BW, Gerhardt HC (2001) Female mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. Behav Ecol Sociobiol 49:443–455

- Schwartz JJ, Buchanan BW, Gerhardt HC (2002) Acoustic interactions among male gray treefrogs, *Hyla versicolor*, in a chorus setting. Behav Ecol Sociobiol 53:9–19
- Smith M, Roberts JD (2003) An experimental examination of female preference patterns for components of the male advertisement call in the quacking frog, *Crinia georgiana*. Behav Ecol Sociobiol 55: 144–150
- Sueur J (2002) Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). Biol J Linn Soc 75:379– 394
- Sueur J, Aubin T, Simonis C (2008) Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18:213–226
- Sullivan BK, Hinshaw SH (1992) Female choice and on male calling behaviour in the grey treefrog *Hyla versicolor*. Anim Behav 44: 733–744
- Vélez A, Linehan-Skillings BJ, Gu Y, Sun Y, Bee MA (2013) Pulsenumber discrimination by Cope's gray treefrog (*Hyla chrysoscelis*) in modulated and unmodulated noise. J Acoust Soc Am 134:3079– 3089
- von Helversen D, Rheinlaender J (1988) Interaural intensity and time discrimination in an unrestraint grasshopper: a tentative behavioural approach. J Comp Physiol A 162:333–340
- Wagner WE (1988) Measuring female mating preferences. Anim Behav 55:1029–1042
- Ward JL, Love EK, O'Bryan LR, Vélez A, Bee MA (2013) Multitasking males and multiplicative females: dynamic signalling in grey treefrogs. Anim Behav 86:231–243
- Welch AM, Semlitsch RD, Gerhardt HC (1998) Call duration as an indicator of genetic quality in male gray tree frogs. Science 280:1928– 1930
- Wells KD, Schwartz JJ (1984) Vocal communication in a neotropical treefrog, *Hylaebraccata:* advertisement calls. Anim Behav 32: 405–420
- Wells KD, Taigen TL (1986) The effect of social interactions on calling energetics in the gray treefrog (*Hyla versicolor*). Behav Ecol Sociobiol 19:9–18
- West-Eberhard MJ (1983) Sexual selection, social competition, and speciation. Q Rev Biol 58:155–183
- Wilczynski W, Brenowitz EA (1988) Acoustic cues mediate intermale spacing in a neotropical frog. Anim Behav 36:1054–1063
- Wyttenbach RA, May ML, Hoy RR (1996) Categorical perception of sound frequency bycrickets. Science 273:1542–1544

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